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Experimental study on the occurrence and activity of soil nematodes in decomposition of plant material

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With 11 figures

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1. Introduction

In recent years many papers have been published summarizing the studies on organic matter decomposition with reference to general problems of this process in terrestrial ecosystems (Swift, Heal & Anderson 1979), the role of all organisms responsible for decomposition (Anderson & Macfadyen 1976, and Coleman *et al.* 1980), and the role of soil fauna alone (Petersen & Luxton 1982). This last paper reports a broad literature review showing that soil animals speed up the mineralization of plant litter. Functioning of the decomposer subsystem depends on the release of biologically important compounds contained in microflora. Soil fauna and, in particular, micro- and mesofauna play an important part in this process. The consumption of microorganisms by soil fauna intensifies nutrient flux, as it has already been found for protozoans, nematodes, and collembolans (grazing on fungi), and also for benthic fauna (after Yeates 1981). The estimation of productivity parameters of animals grazing on decomposer microflora can account for a better understanding of the functioning of the decomposer subsystem. The role of animals in humification and mineralization of organic matter is emphasized by Ryszkowski (1981). He postulates an urgent need for developing the studies of animals living in agroecosystems, including soil animals, through investigation of their metabolic activity.

The present paper is concerned with nematodes, the animal group relatively abundant in soil, feeding on bacteria and fungi and playing an important role in agroecosystems. The studies on the role of nematodes in decomposition processes were reviewed by WASILEWSKA (1980) and YEATES & COLEMAN (1982). The purpose of the present paper is an analysis of changes in a nematode community in relation to losses of dead organic matter exposed in soil, and an estimation of energy flow through soil nematodes. Also some groups of bacterial and fungal flora were observed. In an attempt to get a possibly natural picture of these changes, a field experiment was conducted over a year, in which litter bags were exposed in the soil, and then dead plant material was analysed. Similar experiments were made in Poland earlier but for a shorter period of 16 weeks (WASILEWSKA *et a* . 1981). Among the studies conducted in other parts of the world on the role of nematodes in decomposition using the method of litter bags, two papers should be mentioned (SANTOS *et al.* 1981 and ELKINS & WHITFORD 1982). Both analyse the effect of predation (acarids) on bacteriophagous and mycophagous nematodes. Under arid conditions the elimination of predators was followed by a marked reduction in decomposition due to an increase in the number of bacteriophagous nematodes.

2. Methods

2.1. Experimental design

The experiment was carried out on a large farm (state farm Nowe Sady, Mikołajki county, Suwałki district). The experiment was done in the two variants, samples being exposed at the top and at the base of a terminal moraine, at an altitude of 21 m (upper variant) and 11 m (lower variant) above water level of lake Jorzec, respectively. In this area there were brown soils. Summer barley was grown there in the growing season preceding the experiment. The study began after the harvest (in September). In the following year, potatoes were grown in this area. They were harvested after the experiment had ended.

Post-harvesting residues of summer barley were used in the experiment. They were collected from the field on the third day after harvest. The stalks 20—25 cm long with thicker roots (which length was 3—4 cm) washed with water were air dried to a stable mass. From this material, samples of 150 g were weighed to the nearest 0.05 g and put into bags of 30×30 cm, made of a galvanized metallic mesh-screen with a mesh size of 5×5 mm. Such a big mesh size was used to allow soil fauna a free access. Larger animals, however, could bring or remove material, which could account for an error. A total of 420 samples (210 for each variant) were buried in a horizontal position at a depth of 5—15 cm, what simulates the burying of stubble residues after plowing. The experiment was started in September of 1976. Every four weeks, 15 samples for each variant were taken for analysis over the year (on week 44 samples were destroyed).

2.2. Estimation of organic matter losses

Losses of organic matter were estimated using five samples each time. They were taken to the laboratory, dried at 60 °C for 72 h, and weighed to determine losses in mass. Control samples were processed in the same way to determine losses in the initial material. The content of ash in the material was determined to eliminate the possible bias caused by soil particles that got into the bags. Then the material was homogenized and three samples of 3—4 g each were taken from it and combusted in a muffle furnace at 450 °C.

2.3. Estimation of energy content of the exposed material

The homogenized material was made into pellets. Three 1—1.5 g pellets were made of each sample and combusted in an adiabatic bomb calorimeter. The results obtained were calculated per ash-free dry mass. The energy content of the material generally increased during decomposition processes. The differences between control and the samples of highest energy content amounted to about 10%. An average value of 20.42 $kJ \cdot g^{-1}$ dm was used to express matter losses in energy units.

2.4. Estimation of microflora abundance in litter bags

The number of ammonifying bacteria, Actinomycetes, fungi, and microorganisms utilizing mineral nitrogen was estimated in 1 g dry mass of decomposing matter by means of a dilution plate method on synthetic medium. Fungi were cultured on Martin's medium, Actinomycetes and microorganisms utilizing mineral nitrogen on ammonium starch agar and ammonifying bacteria on agar broth. Standard time and temperatures of microorganisms culture were applied. The material was taken from one litter bag of each series on each sampling date after 8 to 48 weeks of exposure. Thus, this study is of an approximate character.

2.5. Extraction of nematodes from litter bags and surrounding soil

Two litter bags of each variant were used in each sampling period to analyse the nematodes invading them. The content of the bags was put on a dozen or so flat sieves using a modified Baermann's method for extraction (WASILEWSKA 1979). The efficiency of this method is estimated as 80%, presented number of nematodes not corrected. The nematodes obtained from each bag were counted using the Doncaster counting plate. If the "extractory test-tube" contained many nematodes, quantitative subsamples of $^1/_{20}$ or $^1/_{400}$ of its content were analysed. The total number of nematodes was calculated as a mean value for two bags, thus a statistical analysis of the material was not possible.

A homogeneous suspension of nematodes was prepared from each bag separately. From this suspension several portions of nematodes were taken, of which 50 nematodes were selected at random. They were identified to genus under the microscope, and their developmental stage was determined. Their length and width were measured to assess the mean body mass of an individual using ANDRASSY's (1956) method, and also to calculate their biomass. The nematodes identified to genus were classified into trophic groups (WASILEWSKA 1971).

Numbers, trophic structure, and biocoenotic diversity of nematodes living in the soil surrounding the bags were assessed threefold for each variant, in weeks 4, 8 and 24 of the litter bag exposure. Samples of week 4 and 8 are considered as an average because of the similarity in respect of nematofauna. Each time 20 soil cores were taken at random. They were mixed together and 4 subsamples were taken for extraction using the method described elsewhere (WASILEWSKA 1975).

2.6. Estimation of respiratory metabolism (R)

To estimate the respiration of nematode population the data on numbers of bacteriophagous and mycophagous nematodes were obtained from litter bags; individual body masses were taken from subsamples of nematode suspension; and oxygen consumption in bacteriophagous nematodes *Pelodera (Cruznema) monhysteroides* (SKWARRA) DOUGHERTY at different temperatures was taken from KLEKOWSKI & WASILEWSKA (1982). The utilization of the respiration measurements for this species, which is a typical representative of nematodes living in saprobiotic (shortly existing) habitats, has been considered as justified since they were cultured under abundant food conditions KLEKOWSKI & WASILEWSKA 1982), exactly like the nematodes occurring in the exposed litter bags. The same formula was used for the mycophagous nematodes to calculate respiration.

The frequency distribution of individual masses is needed to calculate population respiration. Thus, a histogram was drawn showing the frequency distribution of individuals in particular intervals of body mass. The width of the interval was 0.2 μg, and the mass ranged from 0.0054 μg to 2 μg. A power function of body mass was used to calculate the respiration of individuals of mass corresponding to the central value of successive mass intervals. These values were multiplied by the number of individuals in these intervals. The histogram of mass distribution was constructed for nematodes from the subsamples of nematode suspension from a litter bag. The population density of nematodes in a bag was known. Thus, the total respiration was calculated for nematodes occurring in a bag, on the assumption that the mass distribution and the ratio of bacterio- to mycophagous nematodes in subsamples were identical to those in a bag litter.

Power relationships between respiration and body mass were calculated at three temperatures (KLEKOWSKI & WASILEWSKA 1982):

$$\text{at } 5\ ^\circ\text{C} \qquad R = (1.17 \pm 0.14) \cdot M^{0.46 \pm 0.05}$$
$$\text{at } 10\ ^\circ\text{C} \qquad R = (0.94 \pm 0.08) \cdot M^{0.27 \pm 0.06}$$
$$\text{at } 20\ ^\circ\text{C} \qquad R = (2.15 \pm 0.16) \cdot M^{0.44 \pm 0.04}$$

These equations have been replaced by one power function with parameters a and b, the values of which depended on mean soil temperature at a depth of 5 cm. The least-squares method was used to fit the function:

$$R = a(T) \cdot M^{b(T)}$$

where $a(T) = 0.77 \cdot e^{0.05T}$

$b(T) = 1.29 \cdot 10^{-3} \cdot T + 0.38$

Respiration of nematodes in a litter bag was calculated from the above relationship for mean soil temperatures in the periods between successive sampling dates. To calculate the cumulative oxygen consumption by a nematode community the time of exposure was taken into account.

2.7. Estimation of other productivity parameters

Knowing population respiratory metabolism it is easy to calculate other productivity parameters. If we assume that nematodes have an abundant food supply in bags with dead organic matter (at least in some periods of decomposition), it seems reasonable to apply the data found by DUNCAN *et al.* (1974) for *Plectus palustris*, a bacteriophagous species cultured under abundant food supply. Thus, it has been assumed that R/A = 18% and A/C = 12%, and the cumulative consumption by nematodes was estimated for the study period.

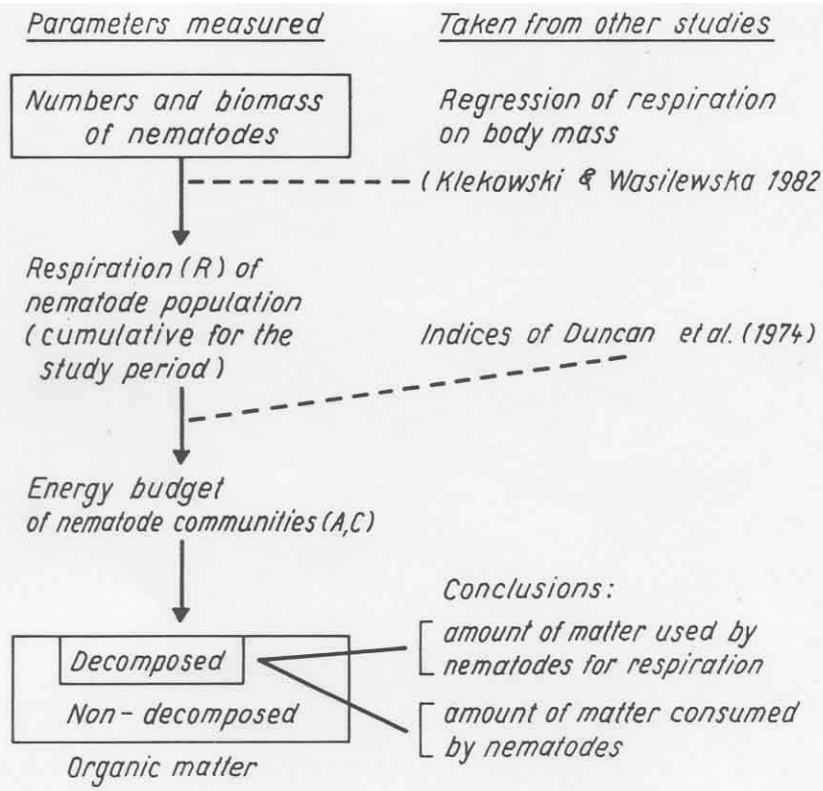
Parameters measured
Taken from other studies
Numbers and biomass of nematodes
Regression of respiration on body mass
(Klekowski & Wasilewska 1982)
Respiration (R) of nematode population (cumulative for the study period)
Indices of Duncan et al. (1974)
Energy budget of nematode communities (A,C)
Conclusions:
Decomposed
amount of matter used by nematodes for respiration
Non-decomposed
amount of matter consumed by nematodes
Organic matter

Fig. 1. The way of estimation of energy flow from dead organic matter to nematodes feeding on bacteria and fungi. Empirical data are enclosed in a frame.

The way for estimating energy flow from dead organic matter in litter bags to nematodes feeding on bacteria and fungi is outlined (Fig. 1).

Table 1. Percentage of different genera of nematodes occurring in experimental litter bags and soil

Upper variant		Genus	Lower variant	
soil	bag		soil	bag
3.1	**46.7**	*Panagrolaimus*	0	**40.0**
3.2	**15.5**	*Rhabditis* s.l.	11.3	**34.0**
4.3	**20.1**	*Aphelenchoides*	2.2	**16.5**
2.4	0.5	*Plectus*	0	0
2.4	0	*Chiloplacus*	0.7	0
0	0	*Eucephalobus*	2.3	0
3.6	0	*Acrobeles*	0	0
0.9	0	*Rhabdolaimus*	0	0
0.9	0	*Cylindrolaimus*	0	0
0.8	0	*Alaimus*	0.8	0
0	0	*Diplogaster* s.l.	0	1
4.3	0	*Aphelenchus*	0.8	1.5
0	0.9	*Paraphelenchus*	0	0
0.8	2.0	*Ditylenchus*	2.5	1
2.1	0.4	*Deladenus*	0	0
1.7	0.4	*Mesodorylaimus*	0	0.5
2.5	0	*Eudorylaimus*	3.2	0
0.8	0	*Drepanodorus*	0	0
0.8	0	*Mononchus*	2.7	0
7.2	5.8	*Acrobeloides*	8.2	1.5
19.3	7.8	*Cephalobus*	**20.5**	3.5
12.3	0	*Tylenchus* s.l.	**3.2**	0
2.2	0	*Helicotylenchus*	0.9	0
6.8	0	*Pratylenchus*	**18.0**	0
16.2	0	*Tylenchorhynchus*	**20.6**	0
22 genera	10 genera		15 genera	9 genera

The mean values for weeks 4 and 8 are compared.

3. Results

3.1. Comparison of nematofauna inhabiting soil and experimental bags

3.1.1. Generic composition and dominance structure

The nematode fauna occurring in soil consisted of 15—22 genera, of which only 9—10 were recorded in litter bags (Table 1). Excluding accidental genera, only plant parasitic nematodes did not occur in bags at all. The other species occurred in both soil and litter bags in differing densities. Dominant nematodes in litter bags, poorly represented in soil, belonged to three genera: *Panagrolaimus* and *Rhabditis* s.l. (bacteriophages), and *Aphelenchoides* (a mycophage) (Table 1). Nematodes of the genus *Cephalobus* were not abundant in bags, but were dominant in soil. The reason of that is difficult to explain.

The percentage of the dominant genera in bags followed specific course in time. Two bacteriophagous nematodes, *Rhabditis* sp. s.l. (obligatory saprobiont) and *Panagrolaimus* (semisaprobiont) dominated in different weeks. The dominance of *Aphelenchoides* sp. increased with decomposition progress (Fig. 2). There is a lack of literature data to compare the observations presented above.

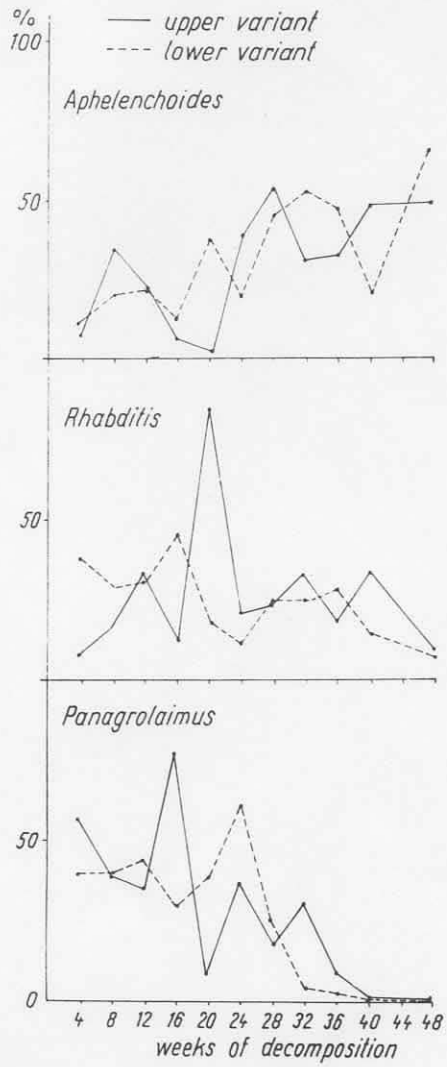

Fig. 2. Changes in the percentage by number of three dominant nematode genera over the experimental period (based on samples of 100 specimens from random portions of nematode suspension from litter bags).

3.1.2. Numbers of nematodes in litter bags and in soil

The exposed litter bags were the place of nematode aggregation and development. This can be seen when comparing nematode population densities in bags and surrounding soil.

In the upper variant the population density of nematodes in soil at a depth of 25 cm was $0.54 \cdot 10^6$ ind · m^{-2} in week 4 of the experiment and $0.68 \cdot 10^6$ ind · m^{-2} in week 8. In the lower variant the two values were similar, fluctuating around $0.68 \cdot 10^6$ ind · m^{-2}. Mean nematode population densities per cm^3 were calculated in soil to a depth of 25 cm and in litter bags (of a size of 20×30 cm and about 4 cm thick after filling them with the post-harvesting residues). For example, the following values were obtained for the upper variant:

week 4: soil — 2.2 ind. cm^{-3}
bag — 1.7 ind. cm^{-3}
week 24: soil — 3.8 ind. cm^{-3}
bag — 195.2 ind. cm^{-3}

3.2. Numbers of nematodes in litter bags over the annual period of decomposition

The number of nematodes occurring in litter bags followed a characteristic course in the annual period of decomposition. No simple correlation was found between nematode numbers and soil temperature or rainfall. Their numbers increased during the first weeks of decomposition in autumn, reaching a peak in week 24 (in March), then they decreased, and increased again until the end of the study period (Fig. 3). An intense reproduction of nematodes occurred in winter, in which there were 20—28 days with snow cover. (The phenomenon of extracting juvenile stages of nematodes from different plants and soil during winter was often observed by the first author. The problem needs more detailed study). The highest numbers were recorded during weeks 12—32. After week 20, juvenile forms

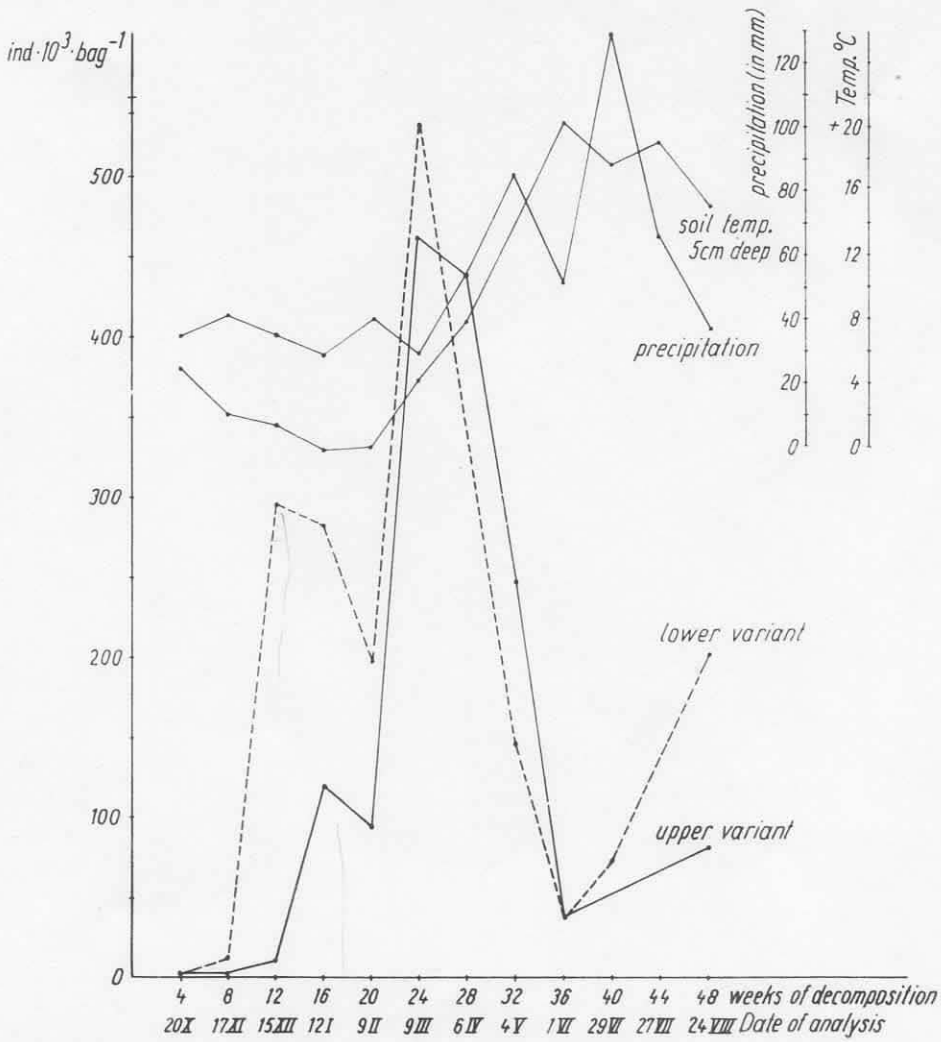

Fig. 3. Number dynamics of nematodes occurring in litter bags.

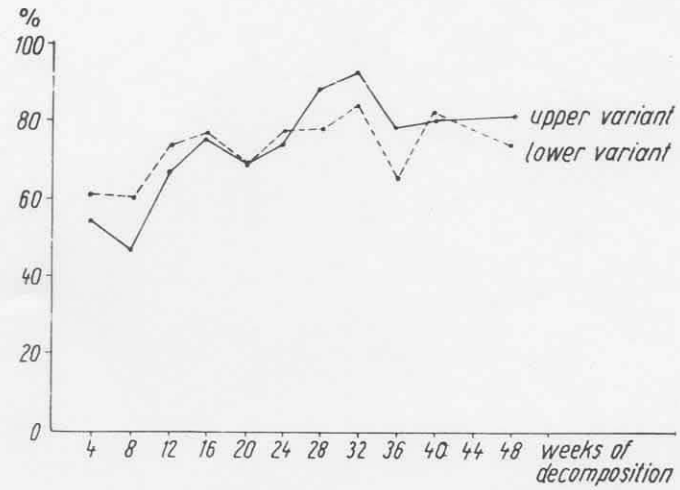

Fig. 4. Proportion of juvenile individuals in whole nematode community.

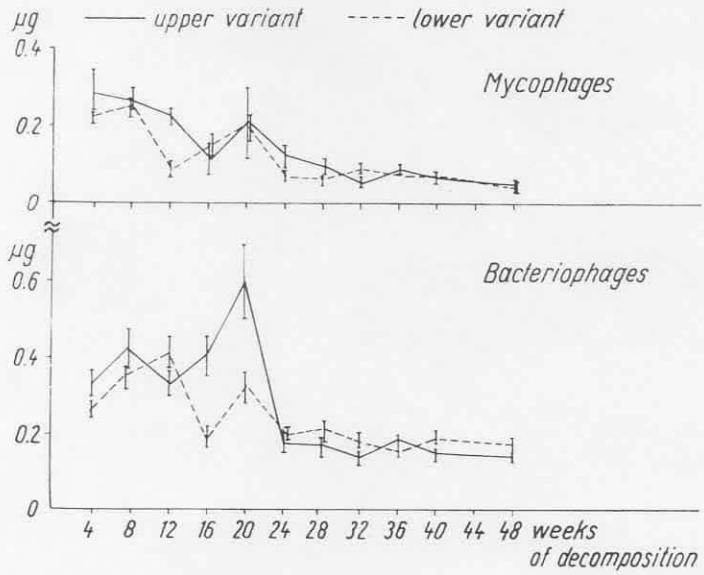

Fig. 5. Mean individual body mass.

were the dominant group, as indicated by their percentage in the community (Fig. 4) and a much lower individual body mass (Fig. 5).

3.3. Trophic structure of nematode communities over the annual period of decomposition

Litter bags were inhabited by nematodes feeding on decomposers (Fig. 6). Until week 32 of decomposition these were almost exclusively bacteriophagous and mycophagous nematodes. In week 32 the community was enriched with pantophages and predators (Fig. 6), which implies that biocoenotic relationships became more complex in litter bags. The ratio of bacteriophagous to mycophagous nematodes varied during 48 weeks of decomposition. In the first period bacteriophages were more abundant, then mycophages predominated (Fig. 7). This was the case in both variants.

3.4. Activity of microflora-grazing nematodes and their food

3.4.1. Bacteriophagous nematodes

The decomposition by bacteria must have proceeded very rapidly, since already in week 8 of exposure the number of ammonifying bacteria and microorganisms utilizing mineral nitrogen was the highest for the whole yearly period. The second, lower peak of these micro-

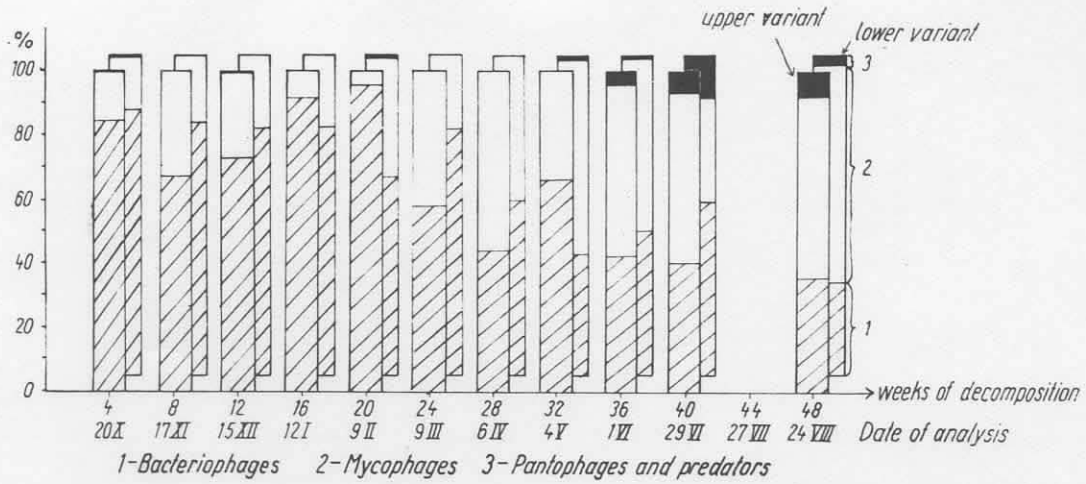

Fig. 6. Proportion of trophic groups in nematode communities occurring in litter bags.

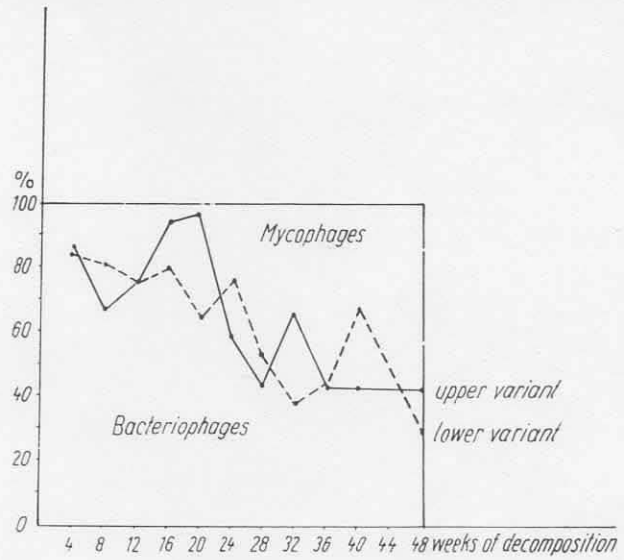

Fig. 7. Ratio of bacterio- to mycophagous nematodes in litter bags in successive weeks of decomposition

organisms occurred between weeks 24 and 32, that is, in spring (Fig. 8). Metabolic activity of bacteriophagous nematodes rose very rapidly between weeks 12 and 16 (January) of decomposition for the upper variant and between weeks 8 and 12 for the lower variant (Fig. 8). Although there were some differences between the two variants, the peak nematode activity in both of them occurred in week 24. This activity was very low in week 36 and slowly increased until week 48. It seems that two stages of the activity of bacteriophagous nematodes can be distinguished. In the first one, which lasted from week 16 to week 20 of exposure, bacterial numbers and nematode number were inversely correlated. It suggest that the increasing nematodes may have caused a decline in bacterial numbers. In the second stage, lasting to the end of the annual experiment, the activity of organisms at these two trophic levels changes in parallel (Fig. 8).

3.4.2. Mycophagous nematodes

Number dynamics of fungi over the 48-week decomposition process is in fact only an index of their potential growth which is indicated by the results of spore germination. But this dynamics allows a conclusion that the first peak of fungal numbers occurred in week 12 of the decomposition (Fig. 9), thus later than the first peak of bacteria numbers. Over the study period there were three peaks of fungal numbers and also three peaks of the activity of mycophagous nematodes (Fig. 9). The second one occurred between weeks 24 and 32, and

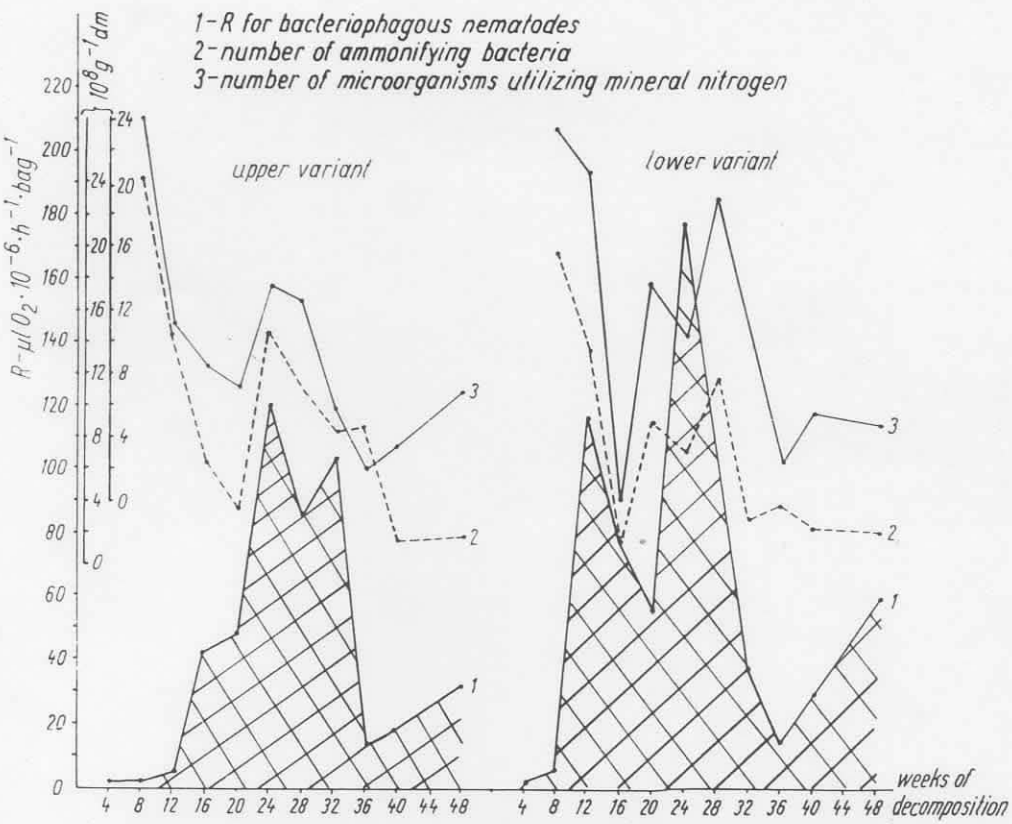

Fig. 8. Metabolic activity of bacteriophagous nematodes (R) in relation to numbers of ammonifying bacteria and microorganisms utilizing mineral nitrogen.

the third one began in the last observation period, that is, in week 48 for nematodes and in week 40 for fungi.

Actinomycetes were much more abundant in the first study period. Their numbers declined from weeks 24—28, and in week 48 they completely disappeared.

3.5. Energy flow in the process of grazing microflora by nematodes

The amount of organic matter decomposed over 48 weeks was 75.4 g dry m · bag^{-1} in the upper variant and 76.8 g dry m · bag^{-1} in the lower variant, that is, respectively 49.4 and 52.5% of the organic matter exposed. The amount of the decomposed organic matter was calculated from the sum of losses in successive weeks of the experiment. During winter and early spring the mass of samples increased in the two variants, probably due to an input of organic matter with ground waters. Consequently, the initial mass taken for calculation has been increased. Microorganisms responsible for the mineralization of the exposed organic matter became a source of food for bacterio- and mycophagous nematodes. Cumulative values of oxygen consumption by nematodes over successive weeks shows that the energy flow through bacteriophages was much larger than that through mycophages (Fig. 10). By week 32 in the upper variant and week 24 in the lower variant, the oxygen consumption in the bacteriophages sharply increased, then markedly dropped, and increased again at the end of the study period. These changes were not so clear-cut for mycophages.

An estimate of the consumption by nematodes associated with decomposition reflects to a large extent this energy contained in organic matter which goes to nematodes through bacteria and fungi. It has been calculated that the cumulative consumption by bacterio- and mycophagous nematodes for 48 weeks was 550—681 kJ · bag^{-1} (Table 2).

The flow of energy through nematodes over the 48-week decomposition period of the exposed organic matter was analysed by relating nematode respiration and consumption to the decomposed organic matter (Table 2). Nematodes consumed, *via* microbial produc-

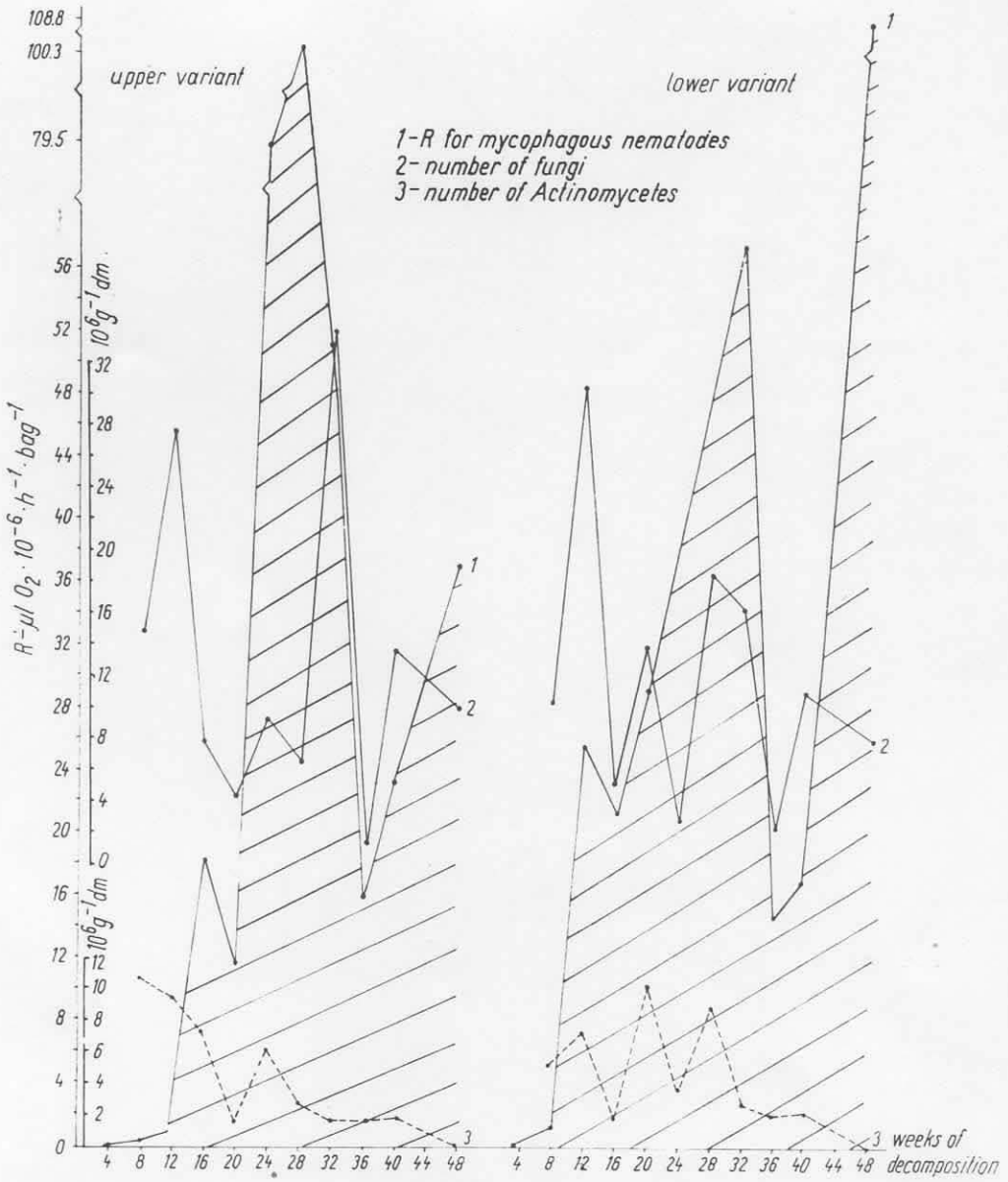

Fig. 9. Metabolic activity of mycophagous nematodes (R) in relation to numbers of fungi and Actinomycetes.

tion, from 36 to 44 % of organic matter decomposed by bacteria and fungi (the value of C), while the energy dissipated from this system by nematodes accounted for a small part of the matter decomposed, which was 0.8—0.9 % (the value of R).

3.6. The effect of catena positions on nematodes and decomposition

Differences between the upper and lower variants corresponded with habitat conditions. In the lower variant there was higher soil moisture and probably higher fertility. The comparisons were not supported by statistical analysis, because of a small number of samples, therefore we can state some trends and watch striking features.

In lower variant it seemed to be a stronger domination of typical saprobiotic nematodes *Rhabditis* s.l. (Table 1), at least in the first 16 weeks of decomposition (Fig. 2). The numbers of nematodes increased quicker in lower variant up to 24 weeks of decomposition (Fig. 3), having in this period higher proportion of juvenile individuals (Fig. 4) and smaller sizes of bacteriophagous and mycophagous nematodes (Fig. 5). The two last features permit to speculate about quicker decomposition rate and quicker nematode population development in lower variant. The tendency in direction to decreased ratio of bacterio- to mycophages in annual course was easy detectable, in spite of differences between two variants

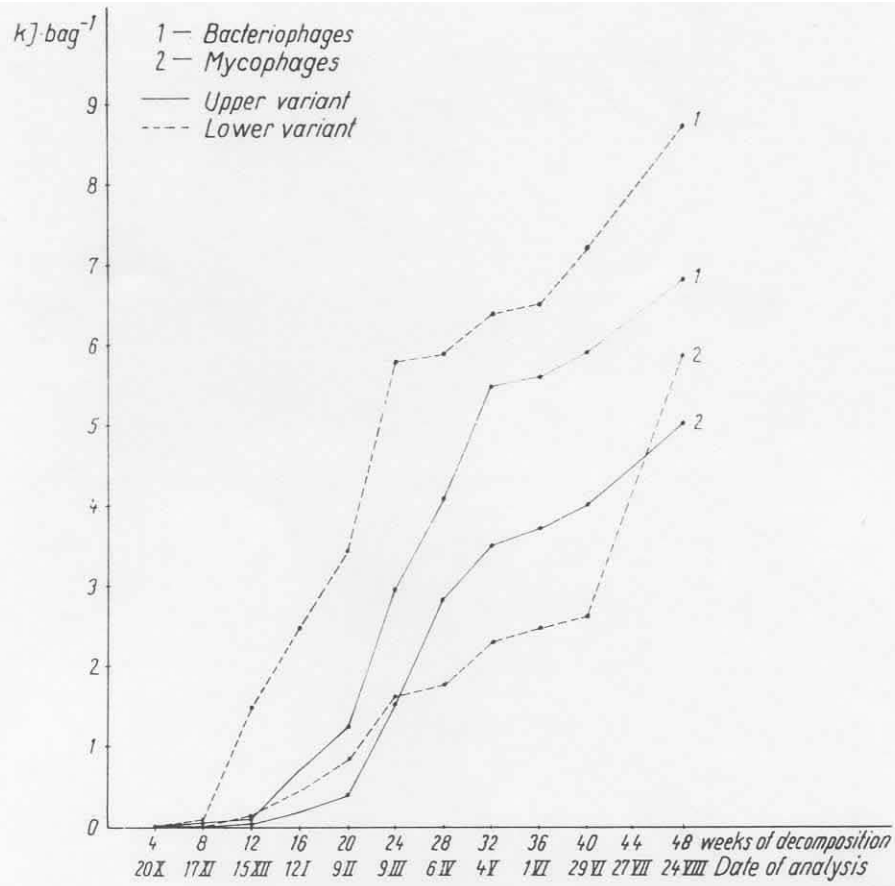

Fig. 10. Cumulative oxygen consumption (R) by bacterio- and mycophagous nematodes during decomposition processes.

Table 2. Energy flow through nematodes over a 48-week period of organic matter decomposition

	Upper variant	Lower variant
Decomposed organic matter		
%	49.4	52.5
g dm · bag^{-1}	75.4	76.8
kJ · bag^{-1}	1,533	1,561
kJ · g^{-1} dm	20.3	20.3
Cumulative R for bacterio- and mycophagous nematodes		
kJ · bag^{-1}	11.9	14.7
kJ · g^{-1} decomposed dm	0.16	0.19
Index: $\frac{\text{Cumulative R}}{\text{Decomposed matter}}$ %	0.77	0.94
Cumulative C for bacterio- and mycophagous nematodes		
kJ · bag^{-1}	550	681
kJ · g^{-1} decomposed dm	7.3	8.8
Index: $\frac{\text{Cumulative C}}{\text{Decomposed matter}}$ %	35.9	43.6

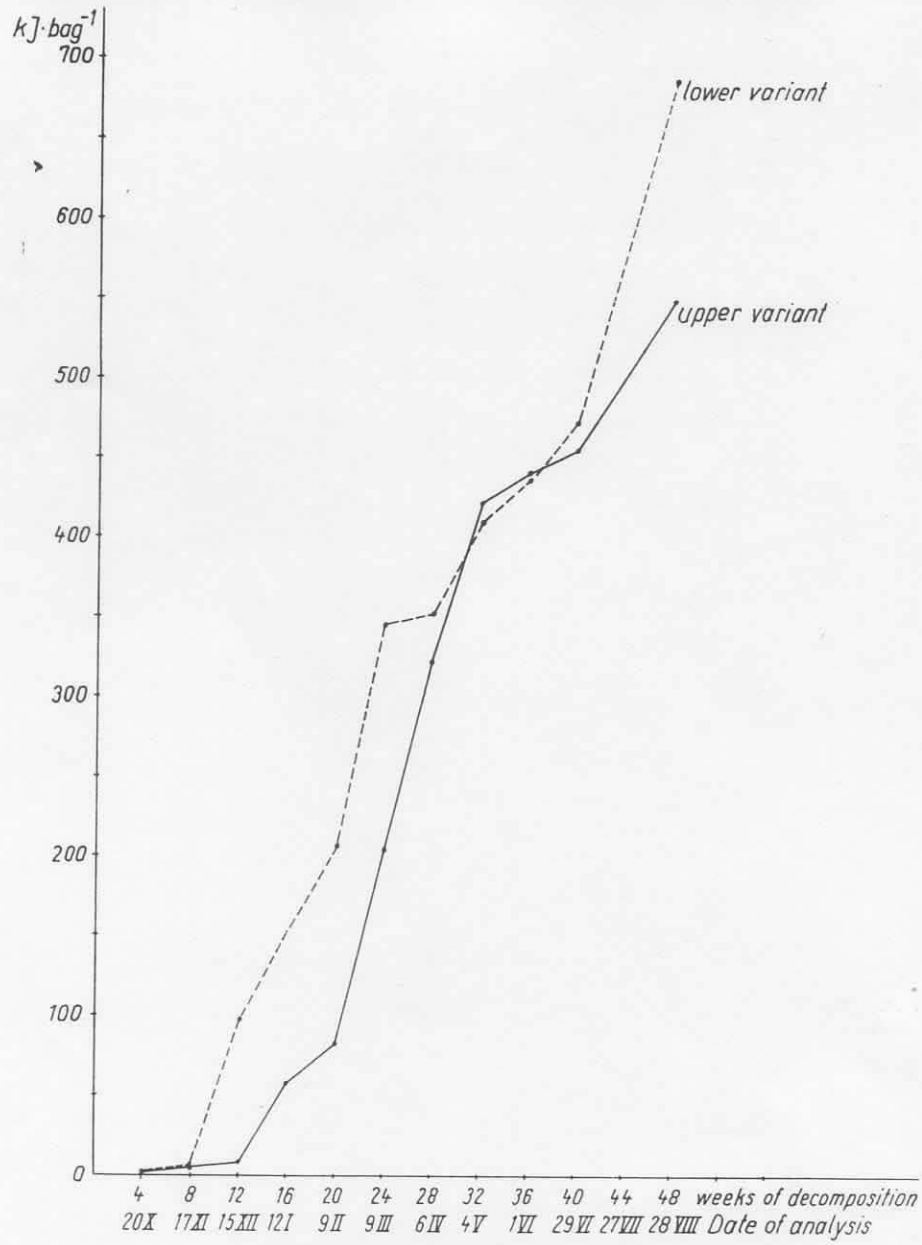

Fig. 11. Cumulative consumption (C) for bacterio- and mycophagous nematodes jointly during decomposition processes.

(Figs. 6 and 7). In the lower variant bacteriophagous nematodes not only became abundant earlier but also their cumulative respiratory metabolism and consumption over the study period were much higher (Figs. 8 and 10, Table 2). This was not the case of mycophagous nematodes (Fig. 9). The curves of cumulative consumption were similar for the two variants over the first two months, differed by weeks 12—28 and then similar again (Fig. 11). Thus, it can be concluded that site conditions influenced the rate of decomposition over the first six months of the process. Differences reappeared at the end of the annual decomposition period.

The influence of catena position on nematodes was first of all reflected in the rate of nematode increase. In the lower variant it was higher and also bacteriophagous nematodes were more abundant than mycophagous.

4. Discussion

Abundant aggregations of bacterio- and mycophagous nematodes in dead organic matter were often observed. Common soil conditions merely support *Rhabditis* populations, while the introduction of bags containing organic matter accounted for a sudden increase in numbers and changes in the age structure of these nematodes (Sohlenius 1973). In an earlier

experiment on decomposition (WASILEWSKA *et al.* 1981), the number of bacterio- and mycophagous nematodes in bags with organic matter was several times higher than in the surrounding soil. A much shorter period of observation (for 16 weeks) does not allow comparison with the present results. Also the plant material exposed was different. In this experiment, roots and fragments of stalks were used, while aboveground plant parts (shoots and leaves) in WASILEWSKA *et al.* (1981). Despite these differences, litter bags in both experiments were dominated by nematodes of the genera *Rhabditis*, *Panagrolaimus*, and *Aphelenchoides*. In the present experiment, *Diplogaster*, *Aphelenchoides*, *Cephalobus* and *Acrobeloides* were not numerous in bags, while they were abundant in the 4-month experiment described by WASILEWSKA *et al.* (1981). It should also be remembered that although the total abundance of all nematodes and particular genera, was determined by food resources in the form of organic matter in bags, it could be limited by predators, as it was indicated by ELKINS & WHITFORD (1982).

Differing and changing abundance of bacteriophagous and mycophagous nematodes requires analysis (Figs. 6 & 7). Bacteria are adapted to colonization of particulate detritus, with a relatively high surface: volume ratio (SWIFT *et al.* 1979). After a rapid initial growth of bacteria, using monosaccharides, pectins, amino acids, the remaining material (mostly cellulose and lignins) is less available. In this second period, the activity of bacteria is lower than in earlier stages. This was observed in the present experiment, in which bacteria reached peak numbers already in week 8 of the annual decomposition period (in week 4 the number of bacteria was not assessed) (Fig. 8). A higher abundance of bacteriophagous nematodes in the first period and mycophagous nematodes in later periods of decomposition probably reflects the food conditions of these animals. The C: N ratio obviously determines the relationship between the occurrence of bacteria and fungi. The C: N ratio, as well as the ratio of C to other nutrients, clearly declines in decomposition processes. SWIFT *et al.* (1979) have found that C: N is 157 for wood, the initial plant material, 26 for saprophagous fungi, and 6 for animals involved in decomposition. The C: N ratio in soil can influence the growth of fungi. It is well known that the saprophytic activity of *Rhizoctonia solani* in soil is intensified when the content of nitrogen is high and that of carbon is low (KREUTZER 1965). In the situation of a higher C: N ratio in bacteriophagous nematodes (from 8: 1 to 12: 1) as compared with that in their food (from 3: 1 to 4: 1), nitrogen is always released as a waste product (ANDERSON *et al.* 1983). One can not exclude the suggestion that an increased feeding activity of bacteriophagous nematodes, through excretion of mineral N, changes the habitat in favour of fungi. Other explanations are also possible. The results obtained by ELKINS & WHITFORD (1982) can be compared with that of present paper. In a "litter bag" experiment on decomposition, they found that the ratio of non-stylet to stylet bearing nematodes was 4: 1 after a month of exposure and 0.8: 1 after a year. Assuming that mainly bacteriophages (nonstylet bearers) and mycophages (stylet bearers) take part in decomposition, we have obtained very similar results. In the present experiment the ratio of bacteriophages to mycophages was 6: 1 after a month, and 0.5: 1 after a year. The similarity of these results is striking, taking into account that experiments were carried out in different ecosystem types, including the semiarid zone (ELKINS & WHITFORD 1982) and the temperate zone (this paper).

The grazing of microflora by soil micro- and mesofauna, including nematodes, was first studied merely a few years ago, when the way of feeding of these animals was unequivocally recognized. Nematodes were not more called detritophages but bacteriophages and mycophages. Only "microcosm" experiments enabled this diagnosis, and also provided a partial explanation for the role of grazing process. It is generally accepted that nematodes feeding on microflora maintain its high abundance and stimulate its activity (ABRAMS & MITCHELL 1980, ANDERSON *et al.* 1981, BÅÅTH *et al.* 1981, TROFYMOW & COLEMAN 1982, ANDERSON *et al.* 1983). They also account for the dispersion of microflora, and increase the degree of organic matter decomposition (ABRAMS & MITCHELL 1980, TROFYMOW & COLEMAN 1982). They stimulate the mineralization of nutrients, this being proved in a microcosm experiment for nitrogen and phosphorus (COLEMAN *et al.* 1977, ANDERSON *et al.* 1979, ANDERSON *et al.*

1981b, Woods *et al.* 1982, Trofymow & Coleman 1982), and due to this, nutrients become available to primary producers (plants) and decomposers (bacteria and fungi) (Anderson *et al.* 1981a). The problem of limiting the development of bacteria in some situations and stimulating in the others as a result of their consumption by nematodes, is not fully understood yet. Some authors argue that bacteriophagous nematodes stimulate the development of bacteria only in soils rich in organic matter; in poor soils, nematode grazing accounts for an earlier occurrence of the period of a natural decline in bacteria (Abrams & Mitchell 1980). Attempts are made to explain this problem by examining direct excretions by grazers (Woods *et al.* 1982). Anderson *et al.* (1983) found a high production of amino acids in experiments with an abundance of bacterial food and an expanding nematode population, and they suggest that this largely stimulates the activity of bacteria. In the present experiments we observed variable numbers of different microflora groups, and also a characteristic course of annual respiratory activity in a nematode community (Fig. 8). These curves suggest that bacterial grazing nematodes have caused a decline in bacterial number but there were also periods in which grazing seemed to stimulate the development of bacteria.

The ratios of production parameters that we accepted after Duncan *et al.* (1974) for a bacteriophagous species *Plectus palustris*, R/A = 18% and A/C = 12%, should be considered as a rough approximation. Recently Schiemer (1982) has found that the R/A ratio for another bacteriophagous nematode, *Caenorhabditis briggsae*, ranged from 15 to 34%, depending on the juvenile: reproductive females ratio in the population. When juvenile individuals prevailed in the habitat, relatively more energy was used for maintenance costs (R) (Schiemer 1982). The cumulative consumption of bacterio- and mycophagous nematodes calculated on the basis of these recent data ranges from 291 to 660 kJ · bag^{-1} for the upper variant and from 358 to 816 kJ · bag^{-1} for the lower variant (compare with data on Table 2). The respective values of consumption by nematodes via microbial production range from 19 to 43% of the decomposed matter in the upper variant and from 23 to 52% in the lower variant. It should be realized that these calculations are made for the situation of abundant food supply, and hence the assimilation coefficient is low (A/C = 12%). Under average soil conditions the A/C ratios for bacterio- and mycophagous nematodes have been calculated to range from 30 to 60% (Sohlenius 1980).

The coefficient of substrate utilization for synthesis of cell material in soil microorganisms depends on the soil type and substrate type. The efficiency of food transformation into plasm of soil microorganisms, the so-called energy coefficient, can reach 80%, but under aerobic conditions in laboratory cultures the assimilation of microorganisms is estimated for about 30% (Gołębiowska 1979, Kaczmarek 1979). In the latter case most of the substrate energy is used for respiration of bacteria. The consumption (C) of bacteria and fungi by nematodes in the present experiment with litter bags has been estimated for 36—44% of the total material decomposed over the year. Thus, it can be expected that a large part of bacterial biomass passes to the next trophic level. Carbon and nitrogen are relatively quickly mineralized in dead microorganisms. This was experimentally confirmed by Marumoto *et al.* (1982), and a resynthesis of live bacterial cells from dead ones was observed by Kaszubiak *et al.* (1976). The study carried out in a pine forest in Sweden shows that independent of low biomass and respiration, bacterio- and mycophagous soil organisms used 30—60% of the annual production of bacteria and fungi in the litter- and humus layer (Persson *et al.* 1980). In other Swedish experiments (Lundgren & Sohlenius, personal communication) it is shown that in the system soil-bacteria-nematodes, the consumption by nematodes accounted for 53% of the total bacterial production in weeks 17—54 of the experiment. As we do not know bacterial production in the present experiment, we could relate nematode consumption only to the decomposed matter. In an earlier, similar experiment, but conducted by only 16 weeks and with a different plant material, nematodes used via microbial production from 8.5 to 36.3% of the decomposed plant material (Wasilewska *et al.* 1981). Thus, if about half of the decomposed material is used by nematodes, their role in the soil should not be neglected.

Analysis of decomposition processes and the role of nematodes in it over a year allows distinguishing some characteristic periods of decomposition. This is a period until week 20 of decomposition and a period after week 20. We will characterize here the second period. After week 20 of decomposition not only the number of nematodes reached highest values (Fig. 3), but also the role of mycophagous nematodes increases (Fig. 7), the proportion of juvenile forms is higher (Fig. 4), and the mean body mass of bacterio- and mycophagous nematodes declines markedly (Fig. 5). These two last facts indicate that turnover of nematodes increases during this period.

Higher soil moisture, and perhaps higher soil fertility, corresponding with lower catena position, have a greater influence on bacteriophagous nematodes (Figs. 3 & 10). A high susceptibility of bacteriophagous nematodes to experimental irrigation and fertilization in a pine forest in central Sweden was noted by SOHLENIUS & WASILEWSKA (1984). The fertilization alone especially reduced the group of mycophagous nematodes. In the present experiment the amount of the organic matter decomposed over a year was similar in the two variants, but in the lower variant the importance of nematodes was a little higher (Table 2). This was mostly due to bacteriophagous nematodes.

5. Summary

Changes were analysed in a community of soil nematodes in relation to losses of dead organic matter exposed in soil. Also the energy flow through soil nematodes during decomposition processes was estimated, and some groups of bacterial and fungal microflora were observed. Dried postharvesting residues of summer barley with roots were put in metallic litter bags with a mesh size of 5×5 mm, and exposed in soil of a harvested barley field, where potatoes were grown the following year. Samples of the exposed material were taken every four weeks over a year to analyse losses of organic matter (by mass), abundance of microflora, and numbers, biomass and faunal composition of nematode communities. These empirical parameters combined with those obtained by other authors were used to estimate the energy flow through nematodes.

We found that nematodes aggregated and reproduced in the exposed organic matter. Dominant nematodes consisted of the genera *Panagrolaimus*, *Rhabditis* s.l., and *Aphelenchoides*. Nematodes of two bacteriophagous genera dominated in different weeks. The dominance of *Aphelenchoides* increased with decomposition processes.

The dynamics of nematodes inhabiting litter bags showed a peculiar course in time. Their numbers increased from the first weeks of decomposition until week 24, then they decreased, and increased again at the end of the annual period.

Bacteriophagous nematodes were more abundant in the first half of decomposition, and mycophagous nematodes in the second half.

Two stages were distinguished in the metabolic activity of bacteriophagous nematodes. In the first stage the bacterial feeding nematodes have caused a decline in bacterial number. In the second stage the activity of these two trophic levels went in parallel. The metabolic activity of mycophagous nematodes followed a different pattern.

About 50 % of the organic matter exposed in the soil was decomposed during 48 weeks. Nematodes consumed, *via* microbial production, from 34 to 44 % of the organic matter decomposed by bacteria and fungi, while the energy dissipated from this system by nematodes accounted for only 0.8—0.9 %.

Habitat conditions to some extent influenced the activity of nematodes in decomposition processes. Higher soil moisture and fertility enhanced the development of bacteriophagous nematodes.

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Synopsis: *Original scientific paper*

Wasilewska, L., & P. Bieńkowski, 1985. Experimental study on the occurrence and activity of soil nematodes in decomposition of plant material. Pedobiologia **28**, 41—57.

Changes were analysed in trophic structure of soil nematode communities in relation to losses of dead organic matter exposed in litter bags into soil. Some groups of bacterial and fungal microflora were observed and their number was correlated with the metabolic activity of bacterial feeding and fungivorous nematodes. Also the energy flow through soil nematodes during one year decomposition processes and the effect of catena positions on nematodes and decomposition were estimated.

Key words: Decomposition, nematoda, bacterial and fungal grazers, energy flow, litter bag method, catena.